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Wilson Bull., 112(1), 2000, pp. 150–153

Perch Proximity Correlates with Higher Rates of Cowbird Parasitism of Ground Nesting Song Sparrows

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ABSTRACT.—The reproductive success of avian brood parasites depends, to a great extent, on their ability to locate host nests that are at the appropriate stages of the host laying cycle. Consequently, brood parasites are expected to possess elaborate mechanisms and search modes to locate potential host nests. Through observing a population of Song Sparrows (*Melospiza melodia*) parasitized by the Brown-headed Cowbird (*Molothrus ater*) we examined two specific factors that may influence cowbird parasitism of a ground nesting host. Proximity to potential perches was a significant predictor of cowbird parasitism, but overhead nest visibility, either classified dichotomously as visible or not, or measured as the absolute area of a nest visible to an observer, was not correlated with the likelihood of parasitism. Comparisons with previous studies suggest that female cowbirds use similar nest searching mechanisms in open habitats, irrespective of the height of host nests. Received 16 April 1999, accepted 23 Aug. 1999.

The reproductive success of avian brood parasites and their effect on host populations depend, to a great extent, on the number of potential host nests and the stage at which host nests are located (Payne 1977, Rothstein 1990). Consequently, there has been considerable effort to determine the cues and search modes that brood parasites use to find nests (Lowther 1979, Thompson and Gottfried 1981, Yahner and DeLong 1992, Vogl et al. 1997, Clotfelter 1998, Teuschl et al. 1998).

The Brown-headed Cowbird (*Molothrus ater*) is a generalist brood parasite known to parasitize more than 220 bird species (Friedmann 1963, Lowther 1993). There is behavioral evidence (Fleischer 1985; but see McGeen and McGeen 1968) and genetic evidence (Alderson et al 1999, Gibbs et al. 1997) that individual female cowbirds may lay eggs in nests of more than one host species. Because the many host species of the Brown-headed Cowbird also build nests at different heights and on many substrates (Lowther 1993, Martin 1993), the mechanisms by which cowbirds find these nests are particularly intriguing.

There are at least four non-exclusive hypotheses proposed to explain the mechanisms and cues used for nest finding by Brown-headed Cowbirds (Lowther 1993, Clotfelter 1998). (1) The nest exposure hypothesis suggests that the more visible the nest of a potential host is, the more likely it is to be parasitized (Martin 1993). (2) The perch proximity hypothesis proposes that female cowbirds are better able to locate host nests when they can observe them from above at a nearby perch (Alvarez 1993, Paton 1994, Romig and Crawford 1995, Clotfelter 1998, Larison et al. 1998). (3) The nesting cue hypothesis asserts that the intensity of host nest defense correlates positively with the proximity of the parasite to the host nest and, thus, the escalation of defensive behavior may serve as a cue for the searching parasite (Smith 1981, Smith et al. 1984, Uye-hara and Narins 1995; but see Gill et al.

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1997). (4) Finally, the host activity hypothesis suggests that vocal and visible activities of hosts associated with territoriality, nest building, and egg laying may attract brood parasites and consequently increase the likelihood of parasitism (Uyehara and Narins 1995, Clotfelter 1998).

Here we report on two specific factors that may relate to the parasitism of ground nesting Song Sparrows (*Melospiza melodia*) by Brown-headed Cowbirds: overhead visibility and distance to potential perches.

METHODS

We studied Song Sparrows and Brown-headed Cowbirds near both units of the Cornell Experimental Ponds in Ithaca, New York in 1998 and 1999 (about 1.5 km², for site description see Hauber 1998). Between April and June 1998 using walk-in traps we trapped and banded 18 female cowbirds in the area, 4 of which were recaptured between April and June 1999 at the same traps. We estimated 30 active Song Sparrow territories (indicated by censuses of singing males and counts of simultaneously active nests) within the fenced boundaries of these sites each year. Song Sparrows breed in Ithaca from early May until mid-July, and they nest along the banks of the ponds and in the surrounding fields mostly on the ground.

The location of each sparrow nest was marked with small pieces of flagging tape about 1 m north and south of the nest. All nests that were depredated during the laying period were excluded from the analyses because we did not know whether these nests had been parasitized. Because we did not observe Song Sparrows reject cowbird, House Sparrow (*Passer domesticus*), or plastic eggs at our study site (Hauber, unpub. data), and because no nests were abandoned upon parasitism (Hauber, in press), we assumed that nests found without cowbird eggs or chicks had not been parasitized.

We found 6 nests during the nest building and laying stages in 1998 and 2 (33%) of these were subsequently parasitized. This proportion was similar to the rate of parasitism of nests found after clutch completion [5 (26%) of 19; Fisher's Exact test; $P > 0.05$] in the same year. Therefore, we do not believe that flagging the nests biased nest discovery by parasites and we included ground nests found both before and after egg laying in our analyses. We monitored nest contents every 24–48 hours between 1 May and 8 June 1998 and 1 May and 31 May 1999. For a different study, we regularly trapped and housed several female cowbirds overnight after these periods, therefore we did not include any later nests in the analyses.

To study nest visibility, we photographed most nests upon discovery with a digital camera (Philips ESP 2/17, picture setting N) from a tripod 0.5 m directly above each nest (1998: $n = 20$, 1999: $n = 3$). We transferred the pictures into a Power Macintosh and

classified each nest as either visible (i.e., part of the nest structure can be seen on the image despite vegetation) or not. We also traced the outlines of the visible portion of each sparrow nest in the photographs and calculated its absolute visible area using NIH Image 1.61 (U.S. National Institutes of Health 1999).

To quantify distance from potential perches, we measured the horizontal distance from the center of each nest found in 1998 to the base of (1) the nearest woody vegetation or permanent object (e.g., fence, nest-box pole) of any height, (2) the nearest woody vegetation or object at least 2 m tall, and (3) the nearest woody vegetation or object at least 3 m tall. We chose these heights to follow the methodology of Clotfelter (1998). Because of the small sample sizes and non-normality of data, we used the non-parametric Fisher's Exact and Mann-Whitney tests in Statview 5.0 (SAS Institute, Inc.) to analyze our data. All values are reported as mean \pm standard deviation.

RESULTS

We found 28 active Song Sparrow nests on the ground at the various stages of the building and laying (9 of 28 nests, 32%), incubating (15 nests, 54%), and nestling (4 nests, 14%) periods, of which 9 nests (32%) were parasitized by cowbirds. Three parasitized nests (33%) had two cowbird eggs and all others had single cowbird eggs.

There was no significant difference between the proportions of visible parasitized nests and visible unparasitized nests (3 visible nests of 7 parasitized nests and 7 visible nests of 16 unparasitized nests; Fisher's Exact test: $P > 0.05$). Neither did the absolute areas visible from directly above each nest differ between parasitized (9.8 ± 16 cm², $n = 7$) and unparasitized nests (8.8 ± 17 cm², $n = 16$; Mann-Whitney test: $U = 53$, $P > 0.05$).

Parasitized nests in 1998 ($n = 7$) were no closer or more distant from the nearest woody vegetation or permanent object than unparasitized nests ($n = 18$; Mann-Whitney test: $U = 44$, $P > 0.05$; Fig. 1). However, parasitized sparrow nests ($n = 7$) were significantly closer than unparasitized nests ($n = 18$) to trees and permanent objects of at least 2 m height (Mann-Whitney test: $U = 28$, $P < 0.034$) and of at least 3 m height (Mann-Whitney test: $U = 24$, $P < 0.018$; Fig. 1). When restricting analyses to nests with hatchlings, parasitized nests ($n = 5$) still tended to be closer to objects of at least 2 and 3 m height (distances: 3.0 ± 3.2 m and 8.1 ± 6.5 m, respectively) than unparasitized nests ($n = 14$, distances: 14

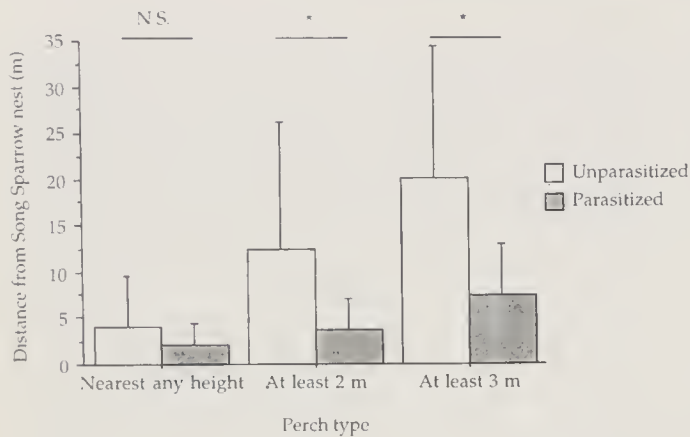


FIG. 1. Comparison of mean distances (+ SD) from parasitized ($n = 7$) and unparasitized ($n = 18$) Song Sparrow nests to the nearest potential perches of any height, and perches at least 2 m and 3 m tall (Mann-Whitney tests: N.S.: $P > 0.05$, *: $P < 0.05$).

± 15 m and 22 ± 15 m, respectively; Mann-Whitney tests: $U = 12$, $P < 0.033$ and $U = 15$, $P < 0.064$, respectively).

DISCUSSION

We tested the predictions of two hypotheses to describe the cues and search modes used by brood parasitic Brown-headed Cowbirds to locate host nests. In contrast to the prediction of the nest exposure hypothesis, we found that overhead nest visibility was not correlated with parasitism of ground nesting Song Sparrows. In support of the perch proximity hypothesis, the mean distances of sparrow nests to the nearest potential perches at least 2 or 3 m tall were significantly closer for parasitized nests.

Previous research on Song Sparrows and Brown-headed Cowbirds showed indirect support for the perch proximity and nest visibility hypotheses (Larison et al. 1998); nests in environments with denser foliage between 2 and 3 m heights (i.e., rich in potential perches) were more likely to be parasitized and nests with denser foliage cover below 1 m (i.e., more limited nest visibility) were less likely to be parasitized.

Recently, Clotfelter (1998) tested several nest searching hypotheses for cowbirds that parasitized open-field nesting Red-winged Blackbirds (*Agelaius phoeniceus*). He found that perch proximity, but not nest exposure, was positively correlated with the likelihood of being parasitized. Using similar methodologies, we found that ground nesting Song

Sparrows showed similar relationships. It is possible that in open habitats female cowbirds use a general sit-and-watch search mode (Smith 1981), regardless of whether the potential host nests are on the ground or above it.

That female cowbirds use high perches for a sit-and-watch strategy in the territories of host species to locate potential host nests has been frequently documented anecdotally (Lowther 1993). In agreement with these observations we found that proximity to tall perches was a significant predictor of cowbird parasitism of ground nesting Song Sparrows. However, we found that overhead nest visibility was not correlated with the likelihood of parasitism. This suggests that female cowbirds may not be locating host nests from these perches by spotting the more exposed nests, instead other factors, such as host activity, may also be important predictors of cowbird parasitism (Clotfelter 1998).

ACKNOWLEDGMENTS

We thank D. Winkler and R. Johnson for the opportunity to work at Cornell Experimental Ponds. For locating nests, assistance in the field, discussions, and comments we are grateful to P. Allen, M. Andrade, M. Armstrong, J. Bower, T. Bruce, A. Clark, C. Clews, T. DeVoogd, S. Emlen, L. Gibbs, A. Krakauer, D. Paprika, B. Petruska, K. Pilz, K. Reeve, S. Rothstein and his lab group, R. Safran, J. Schuetz, P. Sherman, M. Shulman, P. Starks, P. Wildes, D. Winkler and his lab group, P. Wrege, and anonymous referees. This research was supported by a Howard Hughes Predoctoral Fellowship, a Frank M. Chapman Memorial Fund Grant, Sigma Xi grants, the Benning Fund, an Exploration Fund grant of the Explorers' Club, and Cornell University.

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Wilson Bull., 112(1), 2000, pp. 153–155

Male Dickcissels Feed Nestlings in East-central Illinois

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ABSTRACT.—We observed male Dickcissels (*Spiza americana*) commonly feeding nestlings in Conservation Reserve Program (CRP) fields in 1997 in east-central Illinois. Male Dickcissels fed nestlings at six of the eight nests we observed, accounting for 37% of the total nest visits. Overall, females made significantly more nest visits than males. However, at the six male-assisted nests, the number of male and female nest visits did not differ significantly. Male Dickcissel

feeding behavior may have been prompted by low food abundance. Males were not observed feeding nestlings in 1998, when overall nest success was higher and nestling starvation was less than in 1997. *Received 29 March 1999, accepted 15 Sept. 1999.*

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Nearly all male passerines feed their nestlings (Kendeigh 1952, Verner and Willson 1966, Silver et al. 1985). Among North American species, only males of the Dickcissel (*Spiza americana*) and the Boat-tailed Grackle (*Quiscalus major*) do not provide their nestlings with food (Verner and Willson 1969).